

LEAF AND NODAL ANATOMY OF SOME ANDEAN
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ANGIOSPERM LEAVES sometimes provide valuable taxonomic characters. Superficial foliar characteristics that are readily observable, such as pubescence, leaf shape, and type of margin, are in common use and frequently provide diagnostic information. Anatomical characters, on the other hand, are used with less frequency, due partly to their greater uniformity and also to the more elaborate techniques required. Nevertheless, anatomical characters have some desirable attributes which counterbalance their relative inaccessibility in the field. The smaller degree of inter- and intra-specific variability enhances the reliability of differences and makes them more amenable to measurement and therefore more precise. Venation pattern and characters of the node are also useful as sources of information for the taxonomist. Carefully evaluated, they can be used in the interpretation of phylogenetic evolution and adaptive trends.

Phenotypic characters reflect the past evolutionary history of the plant, as well as its present environment, and it is generally agreed that phenotypic characters are adaptive (Mayr, 1942; Stebbins, 1950; Simpson, 1953). Nevertheless it is not always easy to see this, and one should beware of simple anthropomorphic or teleological explanations. Interpretations are devoid of meaning unless they are backed by careful physiological experiments. Likewise, one should avoid interpreting our ignorance about the function of a given structure as a lack of any usefulness.

Angiosperm leaves are one of the most favorable organs in which to study adaptation to diverse environments because they are connected primarily with the water economy of the plant. Adaptation of leaves to conditions of extreme drought has been studied both anatomically and physiologically. Much more study is needed, however, in order to understand the operating selective forces which account for the general adaptive trends. We will need eventually a detailed knowledge of the anatomical features of all species which grow in dry regions, as well as a detailed understanding of the complex ecological conditions which surround their growth.

This paper presents an anatomical and morphological study of the

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leaves and subtending nodes of a group of twenty species in seven related genera. Since these species grow in different, although similar, environments, some insight can be obtained as to the modifications which accompanied the radiation of these species into the extreme conditions of habitats in the high Cordillera de los Andes of South America.

Two of these small genera of Compositae–Astereae are monotypic: *Lepidophyllum cupressiforme* (Lam.) Cassini occurs only in sandy or alkaline soils in southeastern Patagonia and Tierra del Fuego (Cabrera, 1945); *Aylacophora deserticola* Cabrera is known only from the type locality, Plaza Huincul, Prov. de Neuquén, in Argentina (Cabrera, 1953a). Of the other genera, *Parastrephia* Nutt. emend. Cabrera, with five species, grows on the high plateaus (known as *puna*) of southern Perú, southwestern Bolivia, northern Chile, and northwestern Argentina (Cabrera, 1945, 1954a, 1958). The three species of *Chiliotrichiopsis* Cabrera are distributed from the *puna* of northwestern Argentina to the mountains of La Rioja and Mendoza, in the south (Cabrera, 1937, 1944, 1954b). *Nardophyllum* Hook. & Arn., with seven species, occupies the widest geographical range: four species are found in central Chile and the adjacent Prov. de Mendoza in Argentina; two are frequent in Patagonia and southern Chile, ranging from Neuquén to Tierra del Fuego; and one, *N. armatum* (Wedd.) Reiche is a dominant shrub in the climax steppe of the *puna* (Cabrera, 1954a, 1958). The two species of *Chiliophyllum* Phil. have a disjunct distribution, being restricted to Mendoza (*C. densifolium*) and Tierra del Fuego (*C. fuegianum*) respectively. Both species of *Chiliotrichium* Cass. are found in central and southern Chile and neighboring areas of Argentina, from Santiago to Tierra del Fuego (Reiche, 1902). Thus these genera range from Tierra del Fuego, in the southernmost tip of South America, to the highlands of southern Bolivia, a distance of some 4000 km.

All the plants studied are woody shrubs, varying in height from 20 to 150 cm., the majority being about 50 to 100 cm. high. Although none, with the possible exception of *Nardophyllum bryoides*, can be called a true cushion plant, there is a definite tendency in that direction. The branching is dense, the plants form round mats, the leaves are short and crowded, and the inflorescences are borne on short stalks. These characters are more evident in some species than in others. It is hoped that some information may be gained from this study relative to those modifications accompanying adaptation to a pulvinate type of growth in related species.

All observations were made on herbarium specimens. Leaves were cleared according to Foster's technique as explained elsewhere (Solbrig, 1960). Sections of leaves and shoots, expanded in a 2.5% solution of sodium hydroxide for two to six hours, were prepared following the tertiary butyl alcohol method of Johansen (1940) and stained according to the safranin-fast green method (Johansen, 1940). Additional studies were made of hydrated and dried herbarium material.

Both young and mature leaves were studied. Stem material chosen for

sectioning was that of primary and usually very young shoots. More than one node was sectioned in every case. Whenever possible, shoot apices were sectioned and studied.

THE LEAF

External morphology. The leaves of all species studied are small, coriaceous, appressed to the stems or spreading, sessile, spirally arranged (with the exception of the opposite leaves of *Lepidophyllum*), densely hairy on at least one surface, with entire and usually revolute margins. Nevertheless, there are some differences in external aspect which justify description genus by genus.

Leaves of *Nardophyllum genistoides* (Phil.) Gray are linear-lanceolate, 1–1.5 cm. long and 3–4 mm. wide, glandular-pubescent, with entire non-revolute margins. All other species of the genus have linear leaves, varying in length from not more than 5 mm. in *N. bracteolatum* Hauman to almost 2 cm. in *N. chiliotrichioides* (Remy) Gray. The upper surface is glabrous or sparsely pubescent, the lower one densely pubescent. In *N. lanatum* (Meyen) Cabrera both leaf surfaces are white-pubescent. The leaf margins in all these species are strongly revolute and the surfaces are usually very resinous. In two species, *N. bryoides* (Lam.) Cabrera and *N. bracteolatum* Hauman, the leaves are densely crowded on the shoots, the internodes being less than 1 mm. in length.

Parastrephia lucida (Meyen) Cabrera and *P. phylliciformis* (Meyen) Cabrera have relatively large linear leaves, 35 mm. long and 2–4 mm. wide, horizontally curved, and very resinous,² with revolute margins and a pubescent lower surface. *Parastrephia quadrangularis* (Meyen) Cabrera and *P. lepidophylla* (Wedd.) Cabrera have small linear leaves, 3–5 mm. long and 1–2 mm. broad, the lower portions with clasping margins, the tips appressed to the stem, the middle and upper portions with the borders abaxially revolute and the outer surface pubescent. Finally, *P. teretiuscula* (O. Ktze.) Cabrera has small triangular leaves, 1–2 mm. long and 1–2 mm. broad, tightly appressed to the stem, with the outer surface covered with mixed glandular and nonglandular trichomes.

The leaves of *Lepidophyllum cupressiforme* (Lam.) Cassini are opposite, scale-like, appressed to the stem, crescent-shaped, about 1–1.5 mm. long and broad, glabrous and resinous. *Aylacophora deserticola* Cabrera, on the other hand, has ephemeral leaves sparsely arranged on the branches (internodes 5–15 mm. long), linear, 5–15 mm. long and 0.5–1 mm. wide, either woolly or glabrescent.

Chiliotrichiopsis Keidelii Cabrera has linear leaves 3–5 cm. long and up to 1 cm. wide, the upper surface glabrous, and the lower pubescent, with inrolled margins. *Chiliotrichiopsis ledifolia* (Griseb.) Cabrera, in con-

² Fries (1905) states that species of *Parastrephia* (*Lepidophyllum*) *quadrangularis* and *P. phylliciformis* are so resinous that they will readily burst into flame when a match is thrust into the green branches. I have witnessed a similar occurrence with *Gutierrezia Gayana*, a species of similar habit, growing in Chile.

trast, has lanceolate leaves about 3 cm. long and 1–2 cm. broad, the upper surface glandular-pubescent, the lower surface densely so, and the margins not inrolled.

Both species of *Chiliotrichium* have linear-lanceolate leaves that are shiny and sparsely glandular-pubescent on the upper surface, densely pubescent on the lower, and with a revolute margin. The leaves of both are approximately 1–3 cm. long, those of *C. diffusum* Dusén being somewhat broader (3–5 mm.) than those of *C. rosmarinifolium* Less. (1–2 mm.).

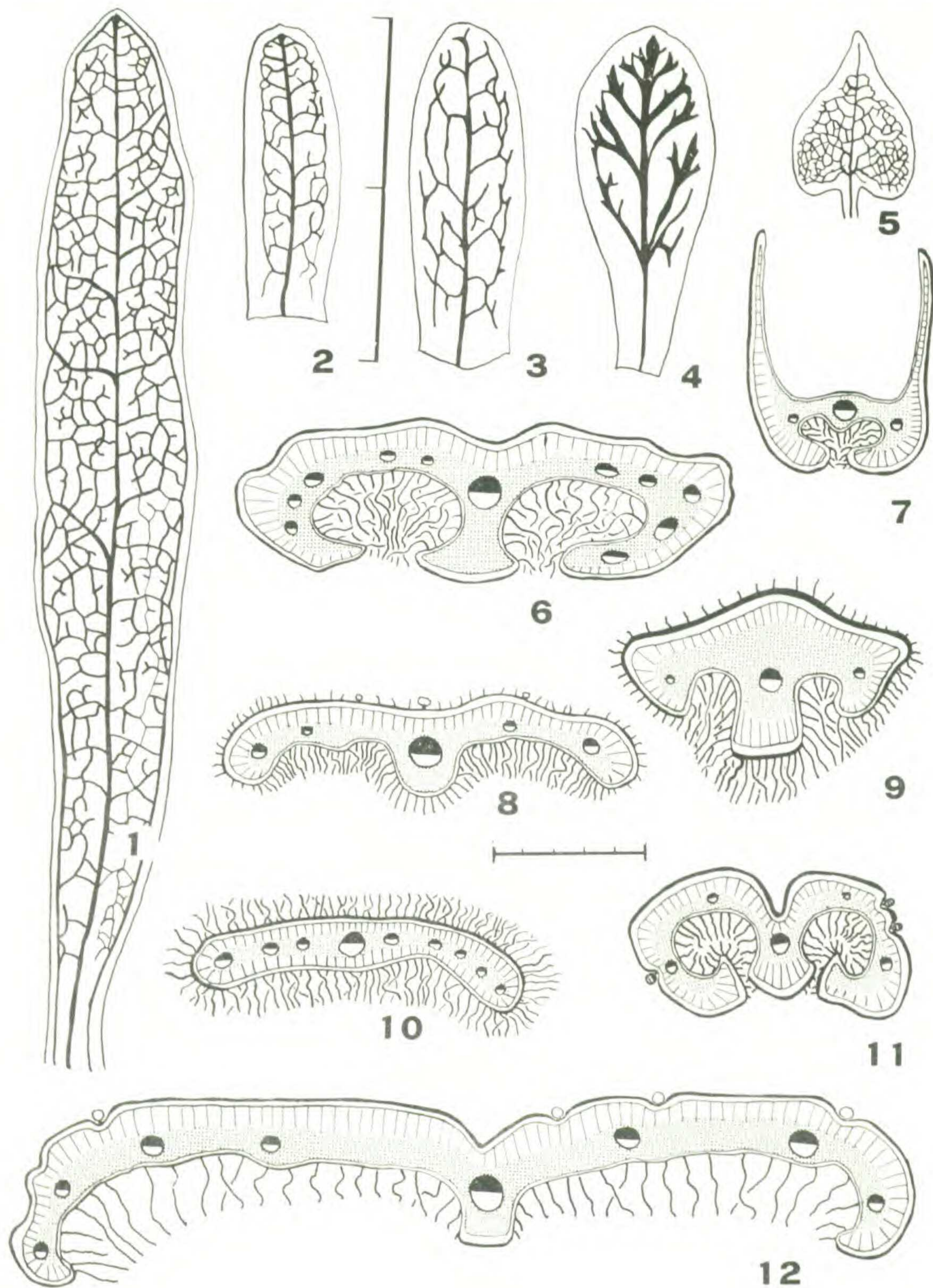
The leaves of both species of *Chiliophyllum* studied are similar to each other: *C. densifolium* Phil. has lanceolate leaves 3–5 mm. long and 2 mm. wide, glabrous on the upper surface, and only slightly glandular-pubescent on the lower; *C. fuegianum* O. Hoffm. has similar leaves 7–8 mm. long and 2–3 mm. wide.

Summarizing briefly it may be said that the leaves of all species studied show such common features as small size, pubescence, and inrolled margins, which are very much in evidence in such species as *Parastrephia teretiuscula* and *Lepidophyllum cupressiforme*, in which the leaves are reduced to small appressed scales.

Venation. The venation pattern shows variations comparable to those observed in the external aspect of the leaf. Here we see a reduced enervation of the lamina and a concomitant increase in sclerification of the veins.

The pattern is basically a reticular one, with a pronounced midvein and two approximately parallel large lateral veins, which often give rise to two more large laterals. The laterals usually are prominent only in the lower third of the lamina, becoming less and less conspicuous toward the tip. This pattern is well represented in leaves of *Chiliotrichiopsis ledifolia* and *Parastrephia lucida*. The first step in vein reduction is a decrease in the number of small veinlets. Types of this sort are the most frequent, and are to be found to varying degrees in *Nardophyllum armatum*, *N. chiliotrichioides*, *N. genistoides*, *N. bracteolatum*, *N. lanatum*, *Parastrephia phylliciformis*, *Chiliotrichiopsis Keidelii* (FIG. 1), *Chiliotrichium diffusum*, and *C. rosmarinifolium*. *Aylacophora deserticola* also possesses this general type of venation, but the veinlets are very thick because of a well-developed sheath of sclereids.

The next step in the apparent reduction series is a gradual disappearance of the two main laterals, so that only the midvein and a few of its branches are left. As we will see this step is associated with changes in the node. In *Nardophyllum bryoides*, *N. obtusifolium* Hook. & Arn. (FIG. 2), *Parastrephia quadrangularis*, and *P. lepidophylla* some traces of the laterals remain, but, on closer examination, it can be seen that they branch off the midvein near its base. In *Chiliophyllum fuegianum* (FIG. 3) and *C. densifolium* (FIG. 4), no trace remains of the laterals, for only the midvein and a few branches, which are highly sclerified in *C. densifolium*, are left. In *Lepidophyllum cupressiforme* and *Parastrephia teretiuscula* (FIG. 5) there occurs lateral development of the reticulum, giving an almost peltate appearance to the lamina. Both species have a well-developed sheath of sclereids surrounding the midvein and the veinlets.



FIGS. 1-6. Leaf venation. Veins in black, differences in width due to sclerenchyma. Each division of scale equals 1 mm. 1, *Chilotrichiopsis Keidelii* (Venturi 3012, A); 2, *Nardophyllum obtusifolium* (Pirion 3360, GH); 3, *Chilophyllum fuegianum* (J. Hunziker 6827, LP); 4, *Chilophyllum densifolium* (Serra 70, LP); 5, *Parastrephia teretiusscula* (Cárdenas 86, GH). FIGS. 6-12. Leaf cross sections. Hairs and glandular hairs represented schematically; cuticle indicated by thick black line, differences in thickness reflecting actual differences; epidermis a white band; palisade parenchyma by horizontal bars; and spongy

Anatomy. The general plan of leaf construction is quite similar in all species studied, as might be expected in closely related genera and species. There are, however, a number of significant differences which will be treated in detail.

For purposes of clarity, four general types will be described; it must be kept in mind, however, that these are artificial and without any evolutionary or phylogenetic significance *per se*.

TYPE A. This might be called the "ericaceous type," because of its similarity to the leaves of certain species of Ericaceae (Hagerup, 1953). The most characteristic features are the strongly inrolled margins and the well-developed midvein region which protrudes considerably on the abaxial surface and forms in connection with the inrolled margins two longitudinal "inner cavities" along the surface of the leaf. These cavities are covered with a very dense mass of hairs (FIG. 20). The general outline in cross section is like that of two contiguous U-beams. This general situation is found in *Nardophyllum bryoides* (FIGS. 25-27), *N. obtusifolium* (FIG. 9), *N. armatum*, *N. bracteolatum*, *N. chilotrichioides* (FIG. 11), *Parastrephia lucida* (FIGS. 13, 20), *P. phylaciformis* (FIG. 15), and *Chilotrichium rosmarinifolium*.

In all these species there is a very thick cuticle, sometimes almost as thick as the epidermis itself, and the epidermis is always simple and composed of large to very large cells. The thick epidermal layer covers the whole upper surface and the outer sides of the inrolled margins (which can present a considerable surface); in addition, it often covers the exposed area of the downward-protruding midvein region. Beneath the epidermis are one to three layers of tightly appressed palisade parenchyma, which occupy about one-half the thickness of the leaf, including the sides. The other half, which faces the "inner cavity," is occupied by one to several layers of spongy parenchyma. The epidermal layer lining the "inner cavity" is relatively thin. Uniseriate multicellular hairs, common in Compositae (Metcalf and Chalk, 1950) are universally present in great profusion in the "inner cavity" and on the upper leaf-surface with varying degrees of density; so also are multicellular, multiseriate glandular hairs (FIGS. 26, 27). The vascular strands in all the leaves, regardless of type, are collateral, and the larger ones are often surrounded by a fibrous sheath. A more detailed description of the vascular bundles will be given later.

The other three leaf types could be interpreted as modifications of Type A, derived by a gradual "unfolding" of the margins. Two different trends or "lines" can be inferred for purposes of description only, since there is no evidence at all to indicate a direct descent, a possibility which indeed seems unlikely.

parenchyma by stipules; outline of leaves drawn with camera lucida. Each division of scale equals 0.1 mm. 6, *Chilotrichiopsis Keidelii* (Fabris & Marchioni 1748, LP); 7, *Parastrephia lepidophylla* (West 7138, GH); 8, *Nardophyllum lanatum* (Morrison & Wagenknecht 17123, GH); 9, *Nardophyllum obtusifolium* (Pirion 3360, GH); 10, *Aylacophora deserticola* (Cabrera 11053, LP); 11, *Nardophyllum chilotrichioides* (Morrison 17321, GH); 12, *Chilotrichium diffusum* (Eyerdam, Beetle & Grondona 24098, GH).

TABLE I. Principal foliar anatomical characteristics

	LEAF POSITION	LENGTH MM.	WIDTH MM.	MARGINS	CUTICLE μ	EXPOSED EPIDERMIS μ	PALI-SADE LAYERS	SPONGY LAYERS	LEAF TRACES
<i>Nardophyllum</i>									
<i>genistoides</i>	horizontal	10-15	3-4	curved	*	*	*	*	3
<i>chiliotrichioides</i>	horizontal	10-20	1-2	convolute	4.5-7.5	13.5-15	1	2-4	3
<i>lanatum</i>	horizontal	5-10	1-2	convolute	6-7.5	15-22.5	1	1-2	3
<i>bracteolatum</i>	horizontal	12	1.5	convolute	1.5-3	22.5-30	1-2	2-4	3
<i>obtusifolium</i>	horizontal	3-4	1	convolute	1.5-4.5	12-15	1	1-3	1
<i>bryoides</i>	horizontal	5	1-2	convolute	1.5-4.5	12-15	2-3	2-3	1
<i>armatum</i>	horizontal	3-10	.5-1.5	convolute	3-4.5	18-25.5	*	*	3
<i>Aylacophora</i>									
<i>deserticola</i>	horizontal	3-10	1-2	straight	1.5? *	*	1-2	3-4	3
<i>Parastrephia</i>									
<i>lucida</i>	horizontal	35	2.5	convolute	4.5-12	18-25.5	1-2	1-2	3
<i>phyliciformis</i>	semiappr.	5	1-1.5	vestigial convolute	6-7.5	15-22.5	1-2	1-2	3
<i>quadrangularis</i>	semiappr.	3-4	1-2	convolute	13.5-16.5	15-22.5	1-2	2-4	3
<i>lepidophylla</i>	appressed	4-5	1-2	convolute	4.5-6	13.5-18	2-4	2-3	1
<i>teretiuscula</i>	appressed	1-2	1-2	curved	3-4.5	15-22.5	2-3	2-3	1
<i>Lepidophyllum</i>									
<i>cupressiformis</i>	appressed	1-1.5	1-1.5	straight	7.5-15	15-22.5	2-4	2?***	1
<i>Chiliotrichiopsis</i>									
<i>Keidelii</i>	horizontal	30-50	3-5	slightly convolute	3-4.5	10.5-15	1-2	1-2	3
<i>ledifolia</i>	horizontal	20-30	5-10	straight	1.5-3	7.5-9	*	*	3
<i>Chiliotrichium</i>									
<i>rosamarinifolium</i>	horizontal	10-20	1-2	convolute	6-12	10.5-15	1-2	1-2	3
<i>diffusum</i>	horizontal	10-20	3-5	slightly convolute	9-10.5	15-18	1-2	1-2	1
<i>Chiliophyllum</i>									
<i>densifolium</i>	horizontal	3-5	1-2	straight	1.5-3	13.5-15	1-2	3-5	1
<i>fuegianum</i>	horizontal	7-8	2-3	straight	4.5-6	10.5-13.5	1-2	3-5	1

* Material does not permit a precise determination.

** Spongy parenchyma consistently broken, forming a large air-filled cavity. Natural or artifact?

TYPE B. The leaves of only four species can be classed here: *Lepidophyllum cupressiforme*, *Parastrephia teretiuscula* (FIGS. 14, 21), *P. lepidophylla* (FIG. 7), and *P. quadrangularis* (FIG. 18). All four species occur under extreme environmental conditions: *Lepidophyllum* on sandy and alkaline soils in the cold southern regions of Patagonia and Tierra del Fuego, and the species of *Parastrephia* on the high *puna* above 3300 meters. The leaves of all four species are appressed to the stems in varying degrees. In *Parastrephia lepidophylla* (FIG. 7) and *P. quadrangularis* (FIG. 18) we find revolute margins and a strongly modified "inner cavity"; in *P. teretiuscula* (FIGS. 14, 21) there is only a small vestige of a

cavity, while in *Lepidophyllum cupressiforme* there is no evidence of a cavity.

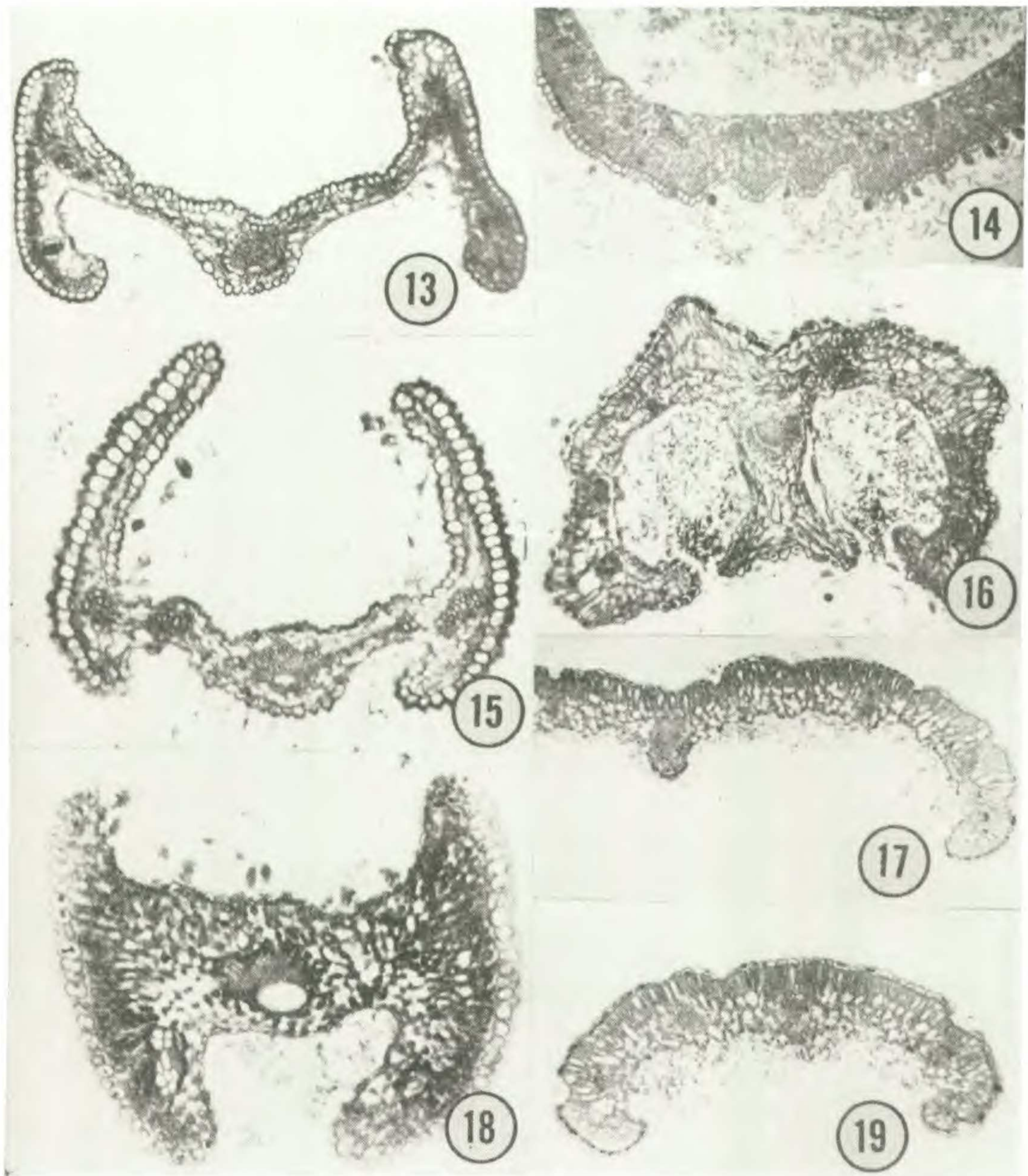
It already has been mentioned that the leaves of all the species under study are sessile and slightly clasping at the base. In leaves of Type B, not only the base but the whole lower half of the leaf partially embraces the stem. The abaxial surface in *Parastrephia* presents two flanges with inrolled margins, so that a transection of the leaf taken somewhere between one-third to one-half the distance from the base resembles a modified "X" (FIG. 15). This presents the problem as to which is the true margin, a question which will be examined in connection with the ontogeny of the leaf.

The abaxial, rather than the adaxial, surface is the one here provided with a thick layer of cutin and a thick, one-layered, large-celled epidermis, subtended by a single row of tightly packed palisade parenchyma. Below the palisade are one or two layers of spongy parenchyma which line the adaxial surface and also the "inner cavity," if the latter is present. The epidermis of the adaxial leaf surface in contact with the stem, as well as that of the "inner cavity" in *Parastrephia lepidophylla* (FIG. 7) and *P. quadrangularis*, is thin and provided with only a thin layer of cuticle. The kinds and disposition of hairs vary from species to species. In *Parastrephia lepidophylla* (FIG. 7) a thick mass of uniseriate multicellular hairs lines the "inner cavity," but is found nowhere else; some multicellular glandular hairs are also found with the nonglandular hairs. In *P. quadrangularis* both the glandular and nonglandular hairs of the same type as in *P. lepidophylla* occur in the "inner cavity," but there is also a strong development of multicellular, multiseriate, stalked glandular hairs as well as of simple hairs, on the adaxial surface, forming a kind of "cement" between leaf and stem. In *P. teretiuscula* (FIGS. 14, 21) there is a complete reversal, with glandular and nonglandular hairs both occurring on the abaxial surface and none on the adaxial surface. Leaves of *Lepidophyllum cupressiforme* are largely devoid of trichomes, and only a few hairs are found on the adaxial surface. It should be mentioned that the leaves of *Parastrephia phylliciformis* (FIG. 15), considered under Type A, are somewhat intermediate between Types A and B.

TYPE C. This category is similar to Type A, but shows a marked simplification. The leaves are horizontally arranged and are generally a little larger, ranging from 10 to 50 mm. in length and from 2 to 10 mm. in width. Five species may be classed here: *Chiliotrichium diffusum*, *Nardophyllum lanatum*, *N. genistoides*, *Chiliotrichiopsis Keidelii*, and *C. ledifolia*.

The midvein region protrudes abaxially (as in Type A) and the leaf margins are revolute. However, since the margins are much less inrolled than in Types A and B and there is a greater horizontal development of the lamina, no so-called "inner cavity" is produced.

The adaxial leaf surface is provided with a thick epidermis, although not so thick as in *Parastrephia lucida* of Type A; neither is the cuticle as thick as in Types A or B. Below the epidermis there is usually one



FIGS. 13-19. Cross sections of leaves to show general outlines. 13, *Parastrephia lucida* (Venturi 4750, GH), \times ca. 22; 14, *Parastrephia teretiuscula* (Cárdenas 86, GH), \times ca. 50; 15, *Parastrephia phylliciformis* (Cabrera 7816, LP), \times ca. 45; 16, *Chilotrichiopsis Keidelii* (Fabris & Marchioni 1748, LP), \times ca. 15; 17, *Chilotrichium diffusum* (Eyerdam, Beetle & Grondona, GH), \times ca. 20; 18, *Parastrephia quadrangularis* (West 6088, GH), young leaf, \times ca. 50; 19, *Chilotrichium diffusum* (Eyerdam, Beetle & Grondona 24098, GH), \times ca. 20 — compare with FIG. 17 from the same collection.

layer of palisade parenchyma succeeded by one or two layers of spongy parenchyma. The lower epidermis is thin and has a thin cuticle. In all species, the abaxial surface has a thick cap of uniseriate multicellular hairs. *Nardophyllum lanatum* (FIG. 8) has hairs also on the upper leaf surface, but not so profusely as on the lower. The glandular trichomes differ from species to species. In *Chilotrichium diffusum* (FIGS. 12, 17, 19) they are numerous and restricted to the upper surface, where they are

embedded in small depressions. In *Nardophyllum lanatum* they are scarce and confined to the adaxial surface. The glandular hairs of *N. genistoides* are peculiar: they are usually uniseriate, consisting of a long stalk (formed by two elongated cells) and a round multicellular head; they extend in rows up to 2 mm. long on the margins and the upper surface. In *Chiliotrichiopsis Keidelii* (Figs. 6, 16) and *C. ledifolia* the glandular hairs are of the common uni- or biseriate, multicellular type already described; they are on the lower surface only in the former species, and on both surfaces in the latter.

Aside from the glandular-hair differences, there are minor variations from species to species in the extent of inrolling of the margins, shape and size of the midvein, and lateral expanse of the blade. *Nardophyllum genistoides* is of special interest. Here the midvein region scarcely protrudes and the margins are only slightly bent. These conditions are very similar to those found in the following type, but there are some important structural differences.

TYPE D. Three species in two genera are treated here: *Aylacophora deserticola*, *Chiliophyllum densifolium*, and *C. fuegianum*. The leaves are small, 3–10 mm. long and 1–3 mm. wide, and linear to oblanceolate. They are thickish in texture and are covered both adaxially and abaxially by an equally thick epidermal layer and a cuticle. A layer of palisade parenchyma lies below the epidermis, which envelopes the leaves on both sides; in the middle of the lamina are one to three layers of spongy parenchyma interspersed with the vascular bundles. *Aylacophora deserticola* (FIG. 10) and *Chiliophyllum fuegianum* are hairy on both surfaces; in *C. densifolium* hairs are completely absent. All three species have glandular hairs on both leaf surfaces. The leaf margins are straight or slightly curved in *C. fuegianum*, the midvein region protrudes only slightly if at all and no "inner cavity" is found.

Vascular bundles. The vascular bundles of all species investigated are normal collateral bundles. All species of *Parastrephia* have an adaxially extended bundle-sheath associated with the midvein, enveloping a duct that is probably a resin canal (Figs. 18, 20, 27). In *P. lucida* this duct is small, but in all other species it is very large and conspicuous. Except in *P. quadrangularis*, no resin canals were observed in primary stems. Species of *Parastrephia* and *Lepidophyllum* lack fibers in association with the vascular bundles. All other genera studied showed some xylary fibers, usually situated at each end of the bundle, or sometimes also between phloem and xylem, or even dispersed between the conducting elements themselves. The midvein of *Chiliotrichiopsis ledifolia* is surrounded by a bundle-sheath formed by one row of extremely large cells of about the same diameter as the radius of the bundle.

THE SHOOT

The primary stems are terete or slightly angled in transection except in species of *Nardophyllum* or *Aylacophora*. In all other genera the thick

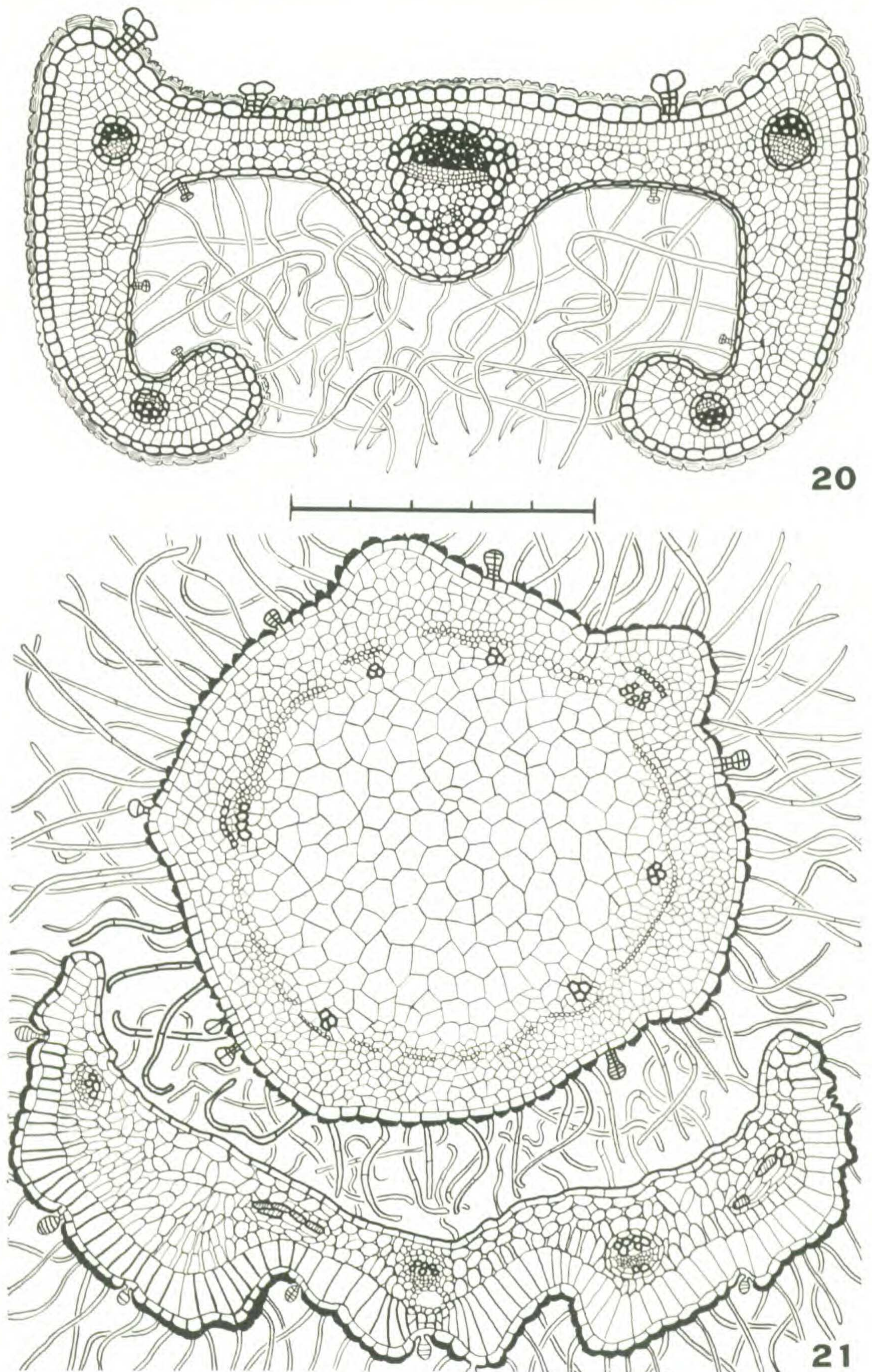


FIG. 20. Camera lucida drawing of cross section of leaf of *Parastrephia lucida* (Venturi 4750, GH), showing anatomical detail; hairs drawn schematically.

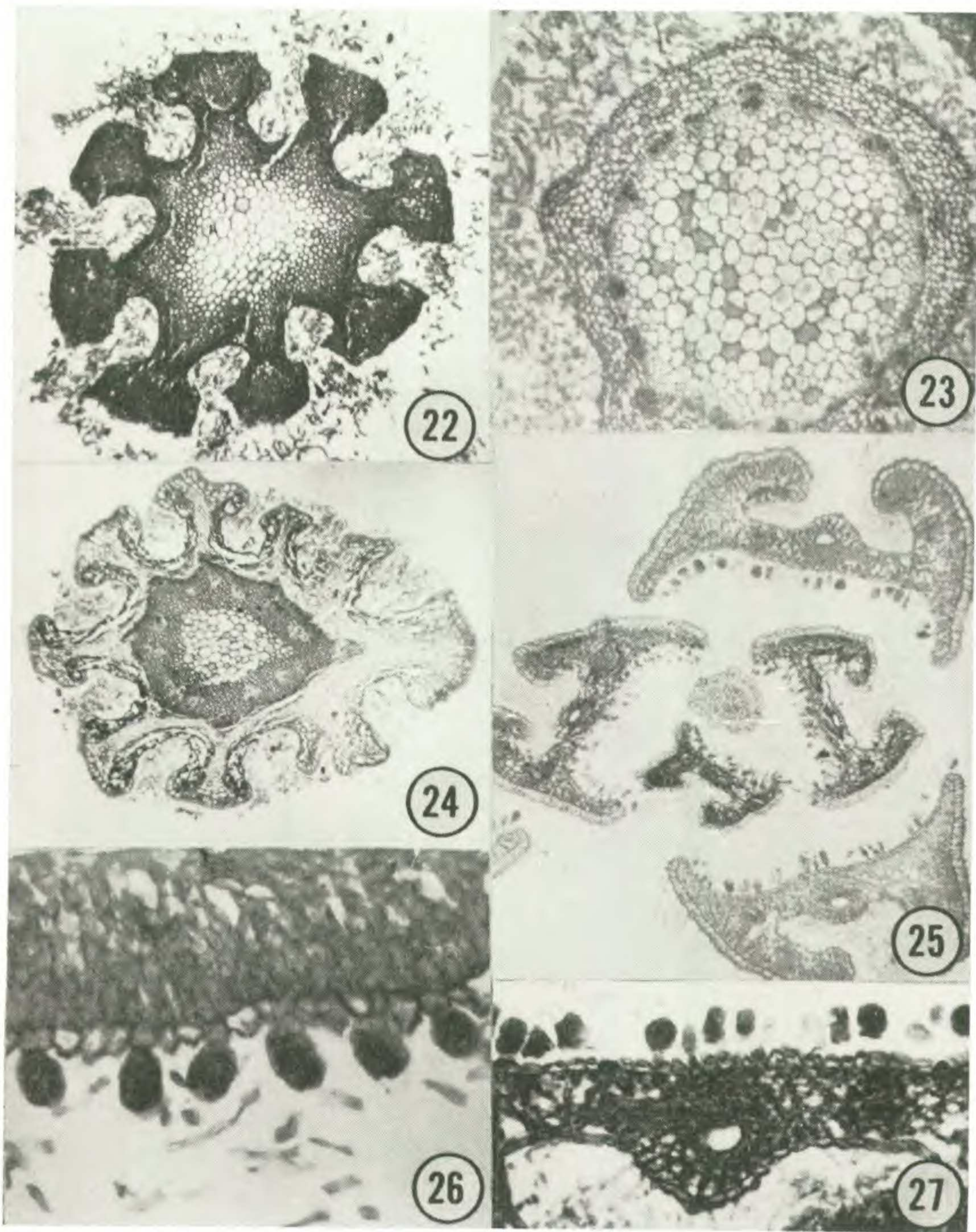
epidermis usually is covered by a thick layer of glandular and nonglandular hairs like those present in the leaves (FIGS. 21 & 23). The cortex is composed of thin, isodiametric cells, and occupies one-third to one-fourth of the diameter of the stem, surrounding a cylinder of collateral bundles. The pith consists of large, thin-walled cells at the center and smaller, thin- or sometimes thick-walled, fiber-like cells on the periphery. In *Parastrephia phylliciformis* the pith is unusually large, occupying over three-quarters of the diameter of the stem.

In all species of *Nardophyllum* the stem is angled or ribbed in transection. The epidermis, cortex, conducting tissues, and pith are similar to those just described. In addition, well-developed strands of sclerenchyma fibers along the ribs add rigidity to the stems. The pith in *Nardophyllum* is also sclerified, especially in *N. armatum*. In *N. bracteolatum* (FIG. 24) and *Aylacophora deserticola* (FIG. 22), deep grooves, reminiscent of the "inner cavity" of the leaf, and also lined with a thick cap of hairs, occur between the ribs. The epidermis is thick and heavily cutinized on the blunt, exposed surface of the ribs, but is thin and only slightly cutinized at the inside of the grooves, where stomata are present. The ribs are abundantly sclerenchymatous peripherally, while the grooves are lined with photosynthetic cortical parenchyma. It is clear that the primary shoots in these species are specialized for photosynthetic activity. In *Aylacophora deserticola*, in which the leaves are few and short-lived, photosynthesis must take place chiefly in the stem.

Nodal anatomy. The number of traces and gaps at the node has been considered to be a character of possible evolutionary significance, especially in woody plants, and may sometimes provide useful taxonomic information. In Compositae, the basic type of node is trilacunar with three traces; this type is basic also for most of the species studied here. Since type of node is usually very consistent in related groups — whole genera and sometimes even whole families — it is interesting to note that in eight of the species studied the node is unilacunar with a single trace, presumably by reduction. Unilacunar nodes have been reported previously in Compositae only for upper leaves in certain genera of Madineae (Carlquist, 1959). Even more remarkable, however, is the occurrence in *Parastrephia*, *Nardophyllum*, and *Chiliotrichium* of species with a trilacunar node and others with a unilacunar node.

Parastrephia phylliciformis, *P. lucida*, and *P. quadrangularis* have a trilacunar node; *P. lepidophylla* and *P. teretiuscula* are unilacunar. *Lepidophyllum cupressiforme* has a unilacunar node with one trace subtending each of the opposite leaves. *Nardophyllum armatum*, *N. genistoides*, *N. bracteolatum*, and *N. chiliotrichioides* all have a trilacunar node with three traces; *N. bryoides* and *N. obtusifolium* are unilacunar with a single trace. *Aylacophora deserticola*, *Chiliotrichiopsis Keidelii*, and *C. ledifolia* have

FIG. 21. Camera lucida drawing of stem and leaf cross section of *Parastrephia teretiuscula* (Cárdenas 86, GH), showing cellular detail. Each division of scale equals 0.1 mm.



FIGS. 22-24. Stem cross sections. 22, *Aylacophora deserticola* (Cabrera 11053, LP), \times ca. 15; 23, *Parastrephia teretiuscula* (Cárdenas 86, GH), \times ca. 20; 24, *Nardophyllum bracteolatum* (Ruiz Leal 7212, LP), \times ca. 15. FIGS. 25-27. Details of leaves of *Nardophyllum bryoides* (Eyerdam, Beetle & Gron-dona 24083, GH). 25, Primordia in different stages of development, \times ca. 50; 26, detail of glandular hairs, \times ca. 100; 27, detail of leaf showing glandular hairs and resin canal, \times ca. 75.

the trilacunar node common to the family. *Chiliotrichium rosmarinifolium* also has a trilacunar node, but that of *C. diffusum* is unilacunar. Finally, both *Chiliophyllum densifolium* and *C. fuegianum* have a unilacunar node with a single trace.

DISCUSSION

In the preceding paragraphs anatomical characters of leaf and node have been described. Their significance from the point of view of adaptation, evolution, and taxonomy remains to be seen. Cushion and mat plants have been the object of intensive investigations in the past, especially studies of an ecological or anatomical nature. An attempt to review the extensive literature is not pertinent to the present study and therefore only some salient information will be pointed out.

Hauri and Schröter (1914, p. 619) defined cushion plants as "perennials, herbaceous or woody, usually green chamaephytes, of spheric, hemispheric, or shingle-like, compact growth. The branches are numerous, with short internodes, covered more or less to the base and without interruption by small, more or less rigid, sessile leaves, withered in various ways. The branches end on the same level and are either closely appressed or the intervening cavities are filled by foreign material. In this manner is produced a certain strength, compactness, and closeness of the individuals, which consist of a living, appressed cover over a spongy mass of decaying material created by the plant itself" (free translation). If we adhere to this definition, none of the species studied can be considered cushion plants. However, Hauri and Schröter also recognized the existence of forms which do not fit their definition but which are nevertheless usually referred to as cushion or cushion-like plants. For these "cushion-like" types they proposed nine different categories. The plants studied here would come under the grouping of "spherical-shrubs" (*Kugelsträucher*), characterized by the loose growth (for cushion plants) of the branches, allowing the passage of air and light into the interior of the plants. In a later study, Hauri (1916) investigated the anatomical structure of leaves and stems of 73 species in 29 genera and 16 families. It is interesting to note that he found a strong convergence in anatomical characters: sessile leaves; a thick epidermis and usually a thick cuticle, or a thick layer of hairs, or both; a well-developed palisade layer; and a relatively slight sclerification of the stem. In this last respect, *Nardophyllum* and *Aylacophora*, of the seven genera investigated, do not agree.

Rauh (1939) presented a very thorough and complete analysis of cushion plants from a morphological point of view. According to him, cushion plants can be defined as "perennial, evergreen plants, with no well-defined central axis and numerous radial, stratified branches, the ends of which form a more or less compact surface due to a similar amount of growth in length" (free translation, p. 269). He divided the "growth-form system of cushion-plants" into seven main types: I. True cushion plants; II. Creeping cushions; III. Turf cushions; IV. Rosette cushions; V. Succulent cushions; VI. Cushion mosses; VII. Monocarpic ("hapaxanthe") cushion plants, that is, annual or biennial forms. He further subdivided these into subtypes. Type I, true cushion plants, was divided into high (radial-high) cushion plants and flat (radial-flat) cushion plants; the first subtype is further subdivided into cushion trees, spheric shrubs,

and hollow cushions. The species studied in the present investigation all fall under the category of spheric shrubs.

Although Rauh did not undertake any anatomical study, he reviewed the different leaf forms of cushion plants and grouped them into different types. Even if a detailed analysis of this classification is not in order here, a few comments may be made about his curved-leaf (*Rollblätter*) type. He characterized it as that in which the lamina, instead of flattening out at maturity, maintains the position it had in the bud. He indicated further that leaves with revolute margins are found only in *Frankenia* and *Anthobryum*, among cushion plants. As can be seen from the present study, revolute margins are more frequent among cushion-like plants (cf. also Cabrera, 1951; Carlquist, 1958). Although, on superficial inspection, the small leaves and inrolled margins might appear to be persistent juvenile forms, this view cannot be supported if the specialized anatomical structure of the leaf is taken into account. Likewise, the contention that sessile leaves in *Anthobryum* are the result of "arrested growth" in the petiole of a related and ancestral *Frankenia* must be discarded. A final word might be added with regard to Rauh's classification of the leaf types in cushion plants. Although a classification of leaf types can be helpful, a formal and complicated subdivision based exclusively on morphological types, regardless of phylogenetic origin, is not conducive to better understanding. When related species, sometimes even of the same genus, have to be separated to fit the classification, it does nothing to clarify taxonomic relationships. Rauh's proposed body types of cushion plants also suffer from the same defect.

Espinosa (1932) made a very careful and complete study of high-montane plants from the Cordillera de los Andes, especially the *páramos* of Ecuador. He recognized four main vegetative types: cushion plants, rosettes, bushes, and spiny bushes (*Dornsträucher*). Rosettes, cushion plants, and shrubs are commonest in the *puna* and *páramos*, spiny shrubs in the deserts of northern Chile and southern Perú, although they are fairly common also in the *puna* and in the "dry *puna*." Of more interest here are his anatomical investigations. He found that high-cordilleran plants generally are protected against desiccation by a thick epidermis and cuticle and a thick layer of hairs. Although none of the species studied by Espinosa shows leaves with the same cross section as those studied here, species with involute- and revolute-margined leaves were found, and also plants with leaves appressed to the stem, and some with large interior air chambers. Similar air chambers were reported for different species of the subantarctic islands of New Zealand by Cockayne (1909). No data on nodal anatomy were presented by Espinosa.

By way of summary, although none of the species studied by me can be considered a "typical" cushion plant, there seems to be general agreement that my material belongs ecologically to a cushion-like category. Some of the foliar features, such as thick epidermis, thick cuticle and compact palisade, appear to be relatively common among both cushion plants and cushion-like plants. On the other hand, the peculiar revolute-

margined leaf of some species of *Parastrephia* and *Nardophyllum* is less common and is only indirectly associated with a cushion habit. This type of leaf is widespread in Ericaceae (Hagerup, 1953), where it is frequently associated with dry habitats, but it is not very common outside that family.

Hagerup (1953), in reviewing the leaves of Ericaceae, considered the revolute projections to be not the true margins of the lamina, but a later outgrowth. This view was challenged by Hara (1956) on ontogenetic grounds. My own observations on shoot apices and primordia appear to confirm Hara's views, although they were not always decisive. Even at very early stages the primordia show configurations correlated with the final shape of the leaf (FIG. 25), and, although there is an increase in size of the revolute projections, they can hardly be interpreted as a "later outgrowth." The point is, in any case, a rather academic one, which depends largely on the particular definition of leaf margin.

Leaf venation in cushion plants has been studied very little. From my study of *Raoulia* (Solbrig, 1960), a New Zealand genus of true cushion plants, it would appear that a strong reduction in leaf venation may accompany the cushion habit in this genus. A similar conclusion is reached in the present study.

Nodal structure in cushion plants has also been neglected. The presence of two nodal types in the same genus is remarkable, and suggests greater flexibility in this character than has usually been assumed. The correlation with other structures suggests that in these Compositae the unilacunar condition is derived, adding to the body of evidence presented by Bailey (1956) that this is a common situation in advanced families of Angiosperms. That the trilacunar situation is always the primitive condition in Compositae cannot be said with certainty.

Although cushion plants are found in most high-montane areas of the world, they are most abundant in certain portions of the Andes of South America, especially the *páramos* of Colombia and Ecuador and the *puna* from Perú southwards, and in Patagonia (Andine Dominion of Cabrera, 1953). In these areas are found about 50 per cent of the pulvinate species known (Hauri and Schröter, 1914). Hauri and Schröter recorded 34 families and 78 genera containing a total of 338 species of cushion plants. Rauh (1939) put the number at about 400 species. Families with the largest number, according to these authors, are Compositae (15 genera, 52 species), Caryophyllaceae (12 genera, 49 species), Umbelliferae (4 genera, 34 species), and Cruciferae (2 genera, 34 species). The independent acquisition of this habit by more than 300 species of so many different families in different parts of the world suggests that this form of growth has some adaptive advantage, and this has been generally assumed. On the other hand, it is not very clear what the exact adaptation might be. The early interpretation was that cushion plants were xerophytic. When it was discovered that they often grow in moist habitats, the concept of "physiological xeromorphy" was developed (Hauri and Schröter, 1914; Hauri, 1917). Experiments by Walter (1931) indicated

for cushion plants on Pikes Peak, Colorado, a low osmotic pressure which discredited the idea of "physiological xeromorphy." Rauh (1939) presented a lengthy discussion of the subject. It suffices to say that different factors probably are operative, and that, although there is undoubtedly a convergence in morphological characteristics, there is no necessity to assume an equal convergence in the physiological responses of the plants. Only careful experiments on a larger number of plants could elucidate this problem. It is also quite clear that the plants show definite local adaptations within the broad environmental limits where they occur. All species considered in the present investigation grow in dry to very dry environments (Cabrera, 1958; Dusén, 1905; Fries, 1907; Skottsberg, 1916; Soriano, 1948), although such species as *Chiliotrichium diffusum* are found also in moister environments (Skottsberg, 1916).

A few words should be said about the possible taxonomic implications of the present work. Cabrera (1954) has considered the relationships of *Nardophyllum* and concluded that it is closely related on the one hand to the South African genus *Pteronia* L., and to *Chiliotrichium* and *Parastrephia* on the other. *Nardophyllum* differs from *Parastrephia* and *Chiliotrichium*, as well as from *Lepidophyllum*, *Chiliophyllum*, and *Chiliotrichiopsis*, by its tubular heads with all flowers perfect, the other genera having ovulate ray flowers, which can be either ligulate or tubular. Anatomically, *Nardophyllum* is separated from the genera mentioned by the possession of cortical sclerenchyma. It shares the tubular head and cortical sclerenchyma with the genus *Aylacophora*; the two genera differ in pappus and shape of achenes, characters which are generally variable within the tribe. There is also remarkable similarity in stem structure between *Aylacophora deserticola* and *Nardophyllum bracteolatum*; the leaf structure, on the other hand, is quite different in *Aylacophora* and *Nardophyllum*. In any case, it seems safe to assume that *Aylacophora deserticola* is closely related to *Nardophyllum*.

Cabrera (1954) separated *Lepidophyllum* and *Parastrephia* because of the opposite leaves, well-developed ray ligules, shortly papillose or glabrous achenes and paleaceous pappus of *Lepidophyllum*, contrasted with the alternate leaves, tubular or shortly ligulate ray flowers, hairy achenes, and bristly pappus of *Parastrephia*. Anatomically, *Lepidophyllum* is similar to *Parastrephia teretiuscula*, the main differences relating to the opposite leaves of the former. It seems likely that the similarities are due to convergence in these two reduced species.

Chiliophyllum and *Chiliotrichiopsis* differ in pappus and achenes: hairy pappus and weakly pubescent achenes in *Chiliophyllum* versus scaly pappus and strongly pubescent achenes in *Chiliotrichiopsis* (Cabrera, 1954). Anatomically, *Chiliophyllum* has a unilacunar node, *Chiliotrichiopsis*, a trilacunar node. This character is difficult to evaluate taxonomically in this group of genera since in *Nardophyllum*, *Parastrephia*, and *Chiliotrichium*, both unilacunar and trilacunar nodes occur in the same genus. The leaves of *Chiliophyllum* are less well developed than those of *Chiliotrichiopsis*.

The flowers of *Chiliophyllum* are also very similar to those of *Chiliotrichium*, the only difference being the color of the ligulate flowers, which are yellow in *Chiliophyllum*, but white in *Chiliotrichium* (Cabrera, 1954). In view of the situation in other genera of the tribe (Keck, 1958) this is a poor distinction. Anatomically there is not much difference, aside from the fact that one species of *Chiliotrichium*, *C. rosmarinifolium* has a trilacunar node.

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